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Influence of Varying Oxygen Tension on the Oxygen Consumption of the Freshwater Mussel *Lamellidens marginalis* (Lamarck) and Its Relation to Body Size

by

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Abstract. The oxygen consumption of the freshwater mussel *Lamellidens marginalis* is related to the oxygen tension of the medium. The total oxygen consumption increases, in general, with size irrespective of oxygen tension and with oxygen tension irrespective of body size. Variations in total and unit oxygen consumption as a function of oxygen tension are considerably less in smaller animals than in larger animals and both decrease drastically at very low oxygen tensions. From the P_c and oxygen-dependence index values it appears that smaller animals are more independent of environmental oxygen and tend to be regulators. Oxygen dependency increases with size, and larger animals show greater dependence of metabolism on oxygen tension and tend to be conformers.

INTRODUCTION

THE INFLUENCE OF declining oxygen tension on oxygen consumption has been studied in several marine and estuarine bivalves, but such studies on freshwater bivalves are relatively few. Most bivalves are supposed to be independent of oxygen tension down to a certain pressure below which oxygen uptake falls to very low levels (VAN DAM, 1938, 1954; GAARDER & ELLIASSEN, 1954; ROTTHAUWE, 1958; NAGABHUSHANAM, 1962; BERG *et al.*, 1962; BAYNE, 1967, 1971, 1973; MOON & PRITCHARD, 1970; MANGUM & VAN WINKLE, 1973; MANGUM & BURNETT, 1975; TAYLOR & BRAND, 1975a; BAYNE *et al.*, 1976; WAITE & NEUFELD, 1977; BOOTH & MANGUM, 1978; DJANGMAH *et al.*, 1980; MACKAY & SHUMWAY, 1980). However, a few bivalves are oxygen conformers, with their oxygen consumption decreasing with declining oxygen tension (EDDY & CUNNINGHAM, 1934; HAMWI, 1969; BAYNE, 1971; LOMTE & NAGABHUSHANAM, 1971; RAO *et al.*, 1974; MANE, 1975; TAYLOR & BRAND, 1975a; MCMAHON, 1979; FAMME & KOFOED, 1980; LOMTE & JADHAV, 1982).

The effect of body size on the relation between oxygen uptake and oxygen tension has been studied in only a few marine bivalves, and the results are inconclusive (BAYNE, 1971; TAYLOR & BRAND, 1975b; FAMME, 1980; MACKAY & SHUMWAY, 1980).

Therefore, the relation between oxygen consumption and oxygen tension was studied in the freshwater bivalve *Lamellidens marginalis,* and the probable influence of body size on this relation was also investigated.

MATERIALS AND METHODS

The specimens collected from local streams were maintained in aquaria filled with water at the laboratory temperature of 26–28°C for 3–4 days to allow adaptation to laboratory conditions.

Oxygen consumption of the animals was studied using the apparatus designed by SAROJA (1959). The apparatus consists of a widemouthed bottle, serving as a respiratory chamber, fitted with a four-holed rubber cork. One inserted tube served as the inlet and connected to the reservoir, while another tube served as the outlet to collect samples. A third tube served as the control tube for maintaining the water level. A thermometer was fixed through the fourth hole for monitoring temperatures. The dissolved-oxygen content in the water samples collected from the apparatus before and after experimentation was determined by Winkler's iodometric method (WELSH &

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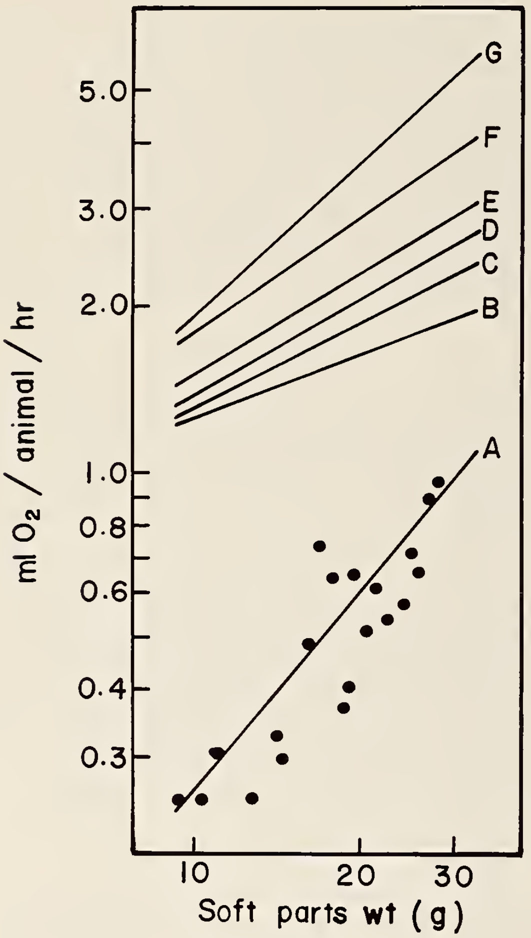

Figure 1

Total oxygen consumption (mL O_2/animal/h) in animals of different sizes measured at different oxygen concentrations of the medium. Temperature ranged from 26 to 28°C. Individual points are indicated for 'A' only. A, 1.13 mL/L (Po_2 = 29.54 mm Hg); B, 2.83 mL/L (Po_2 = 72.47 mm Hg); C, 3.87 mL/L (Po_2 = 101.4 mm Hg); D, 4.91 mL/L (Po_2 = 128.6 mm Hg); E, 5.57 mL/L (Po_2 = 145.96 mm Hg); F, 7.56 mL/L (Po_2 = 197.9 mm Hg); G, 10.20 mL/L (Po_2 = 267.1 mm Hg).

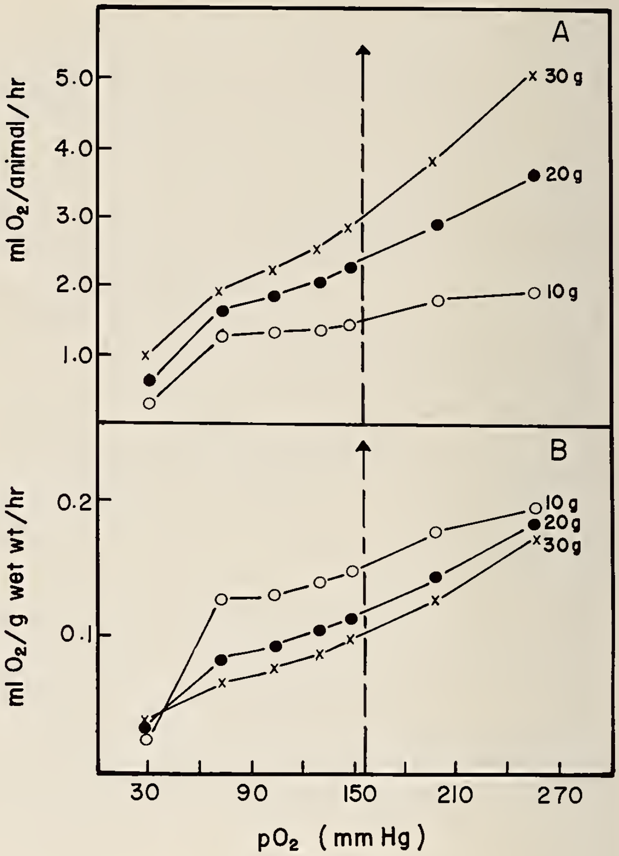

Figure 2

Total metabolism-oxygen tension (A) and unit metabolism-oxygen tension (B) curves plotted for animals of three sizes. Broken line indicates the oxygen tension at air saturation (26–28°C).

SMITH, 1960). From the differences in the oxygen content, the total and unit oxygen consumptions were calculated.

Animals with soft-part weight ranging from 6–30 g were used to cover the natural size range. Animals were brushed thoroughly to remove algal growth over the shells before they were introduced into the respiratory chamber. The soft-part weight was determined at the end of experiments. Oxygen consumption was determined in oxygen-rich medium and then in media of successively decreasing oxygen concentrations. The oxygen content of the medium was changed by pumping either nitrogen or oxygen into it for decreasing and increasing the oxygen content of the medium, respectively. Experiments were carried out at the laboratory temperature of 26–28°C and in the afternoon hours so as to avoid diurnal variations.

Straight lines were fitted to the data plotted on a double logarithmic grid using the method of least squares. Other statistical analyses were carried out using standard procedures.

RESULTS

Oxygen consumption increased with oxygen tension irrespective of size and also with size irrespective of oxygen tension. However, the increase in oxygen consumption with size was not proportional and uniform at different oxygen tensions as indicated by the "b" values. The "b" values decreased gradually from 0.8968 to 0.3734 as oxygen content decreased from 10.2 mL/L to 2.83 mL/L. However, the "b" value increased greatly to 1.1119 when the oxygen content decreased further to the lowest value of 1.132 mL/L (Figure 1, Table 1).

The increase in total metabolism and decrease in unit metabolism as a function of body size were maintained at

Table 1

Regression analysis and correlation coefficient of variations in total metabolism in relation to size in *Lamellidens marginalis*, measured as a function of oxygen concentration (N = 20; level of significance = 95%).

	Oxygen content (mL/L)	Regression analysis		Standard error of b	Correlation coefficient (r)	Level of significance (*P*)	
		A (log a)	b			b	r
A	1.13	−1.6693	1.1199	0.2229	0.8165	<0.001	<0.001
B	2.83	−0.2731	0.3734	0.1189	0.6071	<0.01	<0.001
C	3.87	−0.4206	0.5246	0.0627	0.8085	<0.001	<0.001
D	4.91	−0.4281	0.5646	0.0843	0.7784	<0.001	<0.001
E	5.57	−0.422	0.5932	0.1246	0.8074	<0.001	<0.001
F	7.56	−0.4483	0.6935	0.118	0.8264	<0.001	<0.001
G	10.20	−0.613	0.8968	0.1561	0.833	<0.001	<0.001

all levels of oxygen tension (Figure 2). Furthermore, the variations in total and unit metabolism in relation to oxygen concentration were not proportional and linear, suggesting, thereby, some degree of independence of oxygen consumption on oxygen concentration. However, these variations were greater in larger animals and lesser in smaller animals. Furthermore, the oxygen consumption was greatly depressed when the oxygen content decreased to the very low value of 1.32 mL/L, and this depression was highest in smaller animals. A critical tension or oxygen concentration (P_c) above which there was fairly good regulation of oxygen consumption was more prominent in smaller animals; it was not so clear as body size increased.

It has been observed by earlier workers that P_c is not

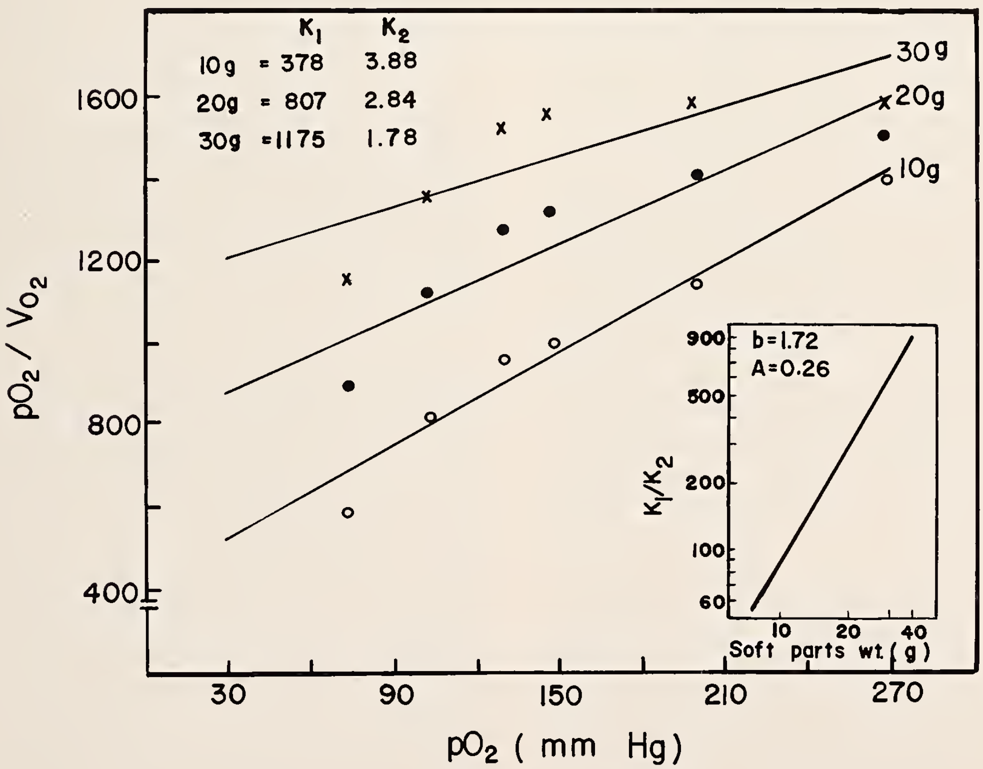

Figure 3

The relation between oxygen tension (Po_2) and the quotient of the oxygen tension and unit oxygen consumption (Po_2/Vo_2) in animals of three sizes (26–28°C). Inset shows the relation between oxygen dependence index and body size.

necessarily a sharp point in oxygen-regulating animals; the metabolism-oxygen curve is often hyperbolic (TANG, 1933). A more reliable estimate of oxygen dependence is obtained by plotting Po_2/Vo_2 against Po_2. Such a plot made for animals of three sizes showed linearity between the two variables. The linearity was not uniform, however, and decreased with increasing size (Figure 3).

The value of K_1/K_2 (where K_1 = Y intercept and K_2 = slope for Po_2/Vo_2 versus Po_2 plots) provides an index of dependence of oxygen consumption on oxygen tension. Higher ratios indicate greater dependence. A plot of K_1/K_2 against body size indicated that the ratio increased with body size (Figure 3).

DISCUSSION

Aquatic animals respond to varying oxygen tension in the surrounding medium either by regulating or conforming their oxygen consumption. All kinds of responses of metabolism to oxygen tension are found in mollusks, ranging from total or partial dependence to complete independence (GHIRETTI, 1966).

Though oxygen uptake in marine bivalves such as *Katelysia opima* (MANE, 1975), *Congeria sallei* (RAO *et al.*, 1974), *Mercenaria mercenaria* (HAMWI, 1969), and *Mytilus edulis* (TAYLOR & BRAND, 1975a; FAMME & KOFOED, 1980) decreases with declining oxygen tension of the medium, imperfect regulation of oxygen uptake over a wide range of oxygen tension is evident in other marine forms. Among these imperfect regulators are *Mya arenaria* (VAN DAM, 1938), *Ostrea edulis* (GAARDER & ELIASSEN, 1954), *Pecten grandis* (VAN DAM, 1954), *Martesia striata* (NAGABHUSHANAM, 1962), *Mytilus perna* (BAYNE, 1967), *Mytilus californianus* (MOON & PRITCHARD, 1970; BAYNE *et al.*, 1976), *Laevicardium crassum* (BAYNE, 1971), *Gelonia ceylonica* (BAYNE, 1973), and *Arctica islandica* (TAYLOR & BRAND, 1975a). Both *Sphaerium simile* (WAITE & NEUFELD, 1977) and *Anadara senilis* (DJANGMAH *et al.*, 1980) are capable of regulating their oxygen consumption within certain limits of environmental oxygen. *Rangia cuneata* (MANGUM & VAN WINKLE, 1973; MANGUM & BURNETT, 1975) is a moderate regulator, whereas in both *Modiolus demissus* (BOOTH & MANGUM, 1978) and *Chlamys delicatula* (MACKAY & SHUMWAY, 1980) regulatory powers are poorly developed.

Information on the metabolic relations of freshwater bivalves to environmental oxygen is sparse. The available literature shows that *Anodonta implicata* (EDDY & CUNNINGHAM, 1934), *Parreysia corrugata* (LOMTE & NAGABHUSHANAM, 1971), *Corbicula fluminea* (MCMAHON, 1979), and *Corbicula regularis* (LOMTE & JADHAV, 1982) are conformers whereas good regulation of oxygen uptake is demonstrated by *Pisidium casertanum* (BERG *et al.*, 1962).

The present study shows that oxygen uptake by *Lamellidens marginalis* increases with the oxygen content of the medium irrespective of body size; but this increase is not proportionate and the relationship is not linear, indicating that there is some degree of respiratory independence of oxygen tension, especially in smaller animals. However, at very low oxygen tensions, oxygen consumption decreases drastically, suggesting the breakdown of oxygen regulatory powers. A critical oxygen tension (P_c), above which there is fair regulation of oxygen consumption, is perceptible in smaller individuals, but not very clear in larger animals. The linear relationship obtained on replotting the data, as per TANG (1933), indicates the same. Thus, the freshwater mussel *Lamellidens marginalis* is neither a strict oxygen conformer like *Anodonta implicata* (EDDY & CUNNINGHAM, 1934), *Parreysia corrugata* (LOMTE & NAGABHUSHANAM, 1971), *Corbicula fluminea* (MCMAHON, 1979), and *Corbicula regularis* (LOMTE & JADHAV, 1982) nor a good regulator like *Pisidium casertanum* (BERG *et al.*, 1962). Rather, it shows some degree of metabolic independence of oxygen tension, leading to some regulation of oxygen consumption in relation to variations in ambient environmental oxygen.

Adequate information is not available regarding the influence of body size on the metabolism-oxygen relationship. Oxygen uptake in *Arctica islandica* is considered oxygen dependent, irrespective of body size (BAYNE, 1971); but a more recent study (TAYLOR & BRAND, 1975b) demonstrates a respiratory independence that increases with increasing body size. Similarly, the situation is not clear in *Mytilus edulis*: K_1/K_2 values decrease with size, indicating that larger individuals show less dependence on oxygen tension than smaller individuals (BAYNE, 1971), while K_m (oxygen dependence index) values suggest that oxygen dependence increases with body weight (FAMME, 1980). Lesser dependence on oxygen tension with size is also evident in *Laevicardium crassum*, where K_1/K_2 also decreases with size (BAYNE, 1971). A relation between the oxygen dependence index and body size is also shown in *Chlamys delicatula* (MACKAY & SHUMWAY, 1980).

The present study shows that the basic relation between metabolism and size is unaltered by oxygen tension. However, "b" values for total metabolism-size curves, and the metabolism-oxygen tension curves plotted for different size groups, indicate a greater influence of ambient oxygen tension on larger animals than on smaller animals. The increase in oxygen consumption with oxygen tension is less in smaller animals and more in larger animals. Interestingly, metabolism is depressed to a greater extent in smaller animals at low oxygen tensions, and this perhaps explains a steep increase in "b" value at low oxygen tension. Increased flattening of both total and unit metabolism-oxygen content curves with decreases in size also illustrates that oxygen uptake in smaller animals tends to be more independent of environmental oxygen and that a tendency toward conformity develops as body size increases, though a dependable correlation between P_c and body size is not evident. However, the linearity of lines plotted as per TANG (1933), and the increase in oxygen dependence index (K_1/K_2) values with size, confirm that there is some degree of respiratory independence of oxygen tension and that this independence decreases with size. The present results agree with those on *Mytilus edulis* (FAMME, 1980) where respiratory independence also decreases with size, but they differ from those on *Mytilus edulis, Laevicardium crassum* (BAYNE, 1971), and *Arctica islandica* (TAYLOR & BRAND, 1975b) where respiratory independence increases with size. It is also clear that respiration is nearly surface-dependent at normal environmental oxygen tensions (4.91 to 7.56 mL/L), whereas it becomes nearly weight-dependent at extreme oxygen tensions (1.132 mL/L and 10.2 mL/L).

The fair degree of respiratory independence of oxygen tension observed in *Lamellidens marginalis* is of ecological significance. Low oxygen conditions are common in streams and ponds during summer months when water levels drop and the water becomes warmer and stagnant. In warm surface waters, both in freshwater and in the sea, there is much photosynthesis, and the oxygen concentration may exceed air saturation (PROSSER, 1973). Respiratory independence under conditions of such varying environmental oxygen would help the animals to maintain a fairly constant metabolic level. Quite interestingly, this ability seems to be better developed in smaller animals, implying that smaller animals can better withstand the rigors of environmental variations.

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